Long-term plant responses to climate are moderated by biophysical attributes in a North American desert

Seth M. Munson[1]*, Robert H. Webb[2], David C. Housman[3], Kari E. Veblen[4], Kenneth E. Nussear[5], Erik A. Beever[6], Kristine B. Hartney[7], Maria N. Miriti[8], Susan L. Phillips[9], Robert E. Fulton[10] and Nita G. Tallent[11]

[1]U.S. Geological Survey, Southwest Biological Science Center, Flagstaff, AZ 86001, USA; [2]School of Natural Resources & the Environment, University of Arizona, Tucson, AZ 85719, USA; [3]Environmental Division, Directorate of Public Works, Fort Irwin, CA 92310, USA; [4]Department of Wildland Resources & Ecology Center, Utah State University, Logan, UT 84322, USA; [5]Department of Biology, University of Nevada, Reno, NV 89557, USA; [6]U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, MT 59715, USA; [7]College of Science, California Polytechnic State University, Pomona, CA 91768, USA; [8]Department of Evolution, Ecology & Organismal Biology, Ohio State University, Columbus, OH 43210, USA; [9]U.S. Geological Survey, Forest & Rangeland Ecosystem Science Center, Corvallis, OR 97330, USA; [10]Desert Studies Center, California State University, Baker, CA 92309, USA; and [11]National Park Service, Mojave Desert Inventory & Monitoring Network, Boulder City, NV 89005, USA

Summary

1. Recent elevated temperatures and prolonged droughts in many already water-limited regions throughout the world, including the southwestern United States, are likely to intensify according to future climate-model projections. This warming and drying can negatively affect perennial vegetation and lead to the degradation of ecosystem properties.

2. To better understand these detrimental effects, we formulate a conceptual model of dryland ecosystem vulnerability to climate change that integrates hypotheses on how plant species will respond to increases in temperature and drought, including how plant responses to climate are modified by landscape, soil and plant attributes that are integral to water availability and use. We test the model through a synthesis of fifty years of repeat measurements of perennial plant species cover in large permanent plots across the Mojave Desert, one of the most water-limited ecosystems in North America.

3. Plant species ranged in their sensitivity to precipitation in different seasons, capacity to increase in cover with high precipitation and resistance to decrease in cover with low precipitation.

4. Our model successfully explains how plant responses to climate are modified by biophysical attributes in the Mojave Desert. For example, deep-rooted plants were not as vulnerable to drought on soils that allowed for deep-water percolation, whereas shallow-rooted plants were better buffered from drought on soils that promoted water retention near the surface.

5. *Synthesis.* Our results emphasize the importance of understanding climate–vegetation relationships in the context of biophysical attributes that influence water availability and provide an important forecast of climate-change effects, including plant mortality and land degradation in dryland regions throughout the world.

Key-words: aridity, climate change, deserts and dryland ecosystems, drought impacts, ecohydrology, land degradation, Mojave Desert, plant species cover, plant–climate interactions

Introduction

Land managers, scientists and policy-makers share a growing concern that rates of land degradation in dryland regions will accelerate with global change and threaten the ecological services provided by 41% of the terrestrial land surface that is currently water limited (UNCCD 1994; MEA 2005; IPCC 2013). Losses of perennial vegetation cover due to climate and land-use changes can lead to declines in productivity, diversity and soil resources upon which two billion humans who live in dryland regions depend (Munson, Belnap & Okin 2011; Ratajczak, Nippert & Collins 2012). Global-change

forecasts in many dryland regions, including the southwestern United States, indicate that there will be further increases in aridity (Seager *et al.* 2007), which, when coupled with large increases in human population (MEA 2005; USCB 2013), could accelerate land degradation. To mitigate and adapt to the consequences of land degradation, there is a fundamental need to understand how plant species in water-limited ecosystems respond to increasing temperatures and reductions in precipitation.

The Mojave Desert is an ideal place to study climate–plant relationships in the context of increasing aridity because it contains some of the driest regions in North America and is representative of deserts globally (Smith, Monson & Anderson 1997). The effects of climate change may be magnified in the Mojave, where plants are water limited by one season of precipitation and protracted droughts. Warming trends in the Mojave Desert began in the late 1970s, and the last century has been punctuated by several drought periods, including the early 21st-century drought that had large precipitation shortfalls during winter months (Redmond 2009; Cayan *et al.* 2010). This warming and drying trend is likely to persist because climate-model projections for 2100 indicate 3–5° C increases in annual temperatures and 5–10% decreases in annual precipitation compared to historical conditions (1971–2000; Cayan *et al.* 2013). The paleontological and historical records (Beatley 1974a; Cole & Webb 1985; Hereford, Webb & Longpré 2006; Miriti *et al.* 2007), coupled with experimental studies (Smith *et al.* 2000), reveal shifts in plant abundance and composition attributable to changes in climate and CO_2, but these impacts can be slow due to infrequent plant establishment, low growth rates and extended individual-plant longevity (Cody 2000).

MODEL OF DRYLAND ECOSYSTEM VULNERABILITY TO ELEVATED TEMPERATURE AND DROUGHT

Understanding future water availability has largely relied on temperature and precipitation forecasts based on future greenhouse-gas concentrations (IPCC 2013). Although water availability is a function of climate, biophysical attributes of dryland ecosystems can strongly regulate the timing, distribution and use of water by plants. We hypothesize that landscape, soil and plant attributes that increase water input and retention or decrease water loss following periodic wetting events will reduce plant vulnerability to future warming and drying in already water-limited regions. To formulate this hypothesis, we integrate previous knowledge of the biological and physical attributes that affect plant-water availability and use into a conceptual model (Fig. 1) on the vulnerability of plant species and functional types to elevated temperature and drought. The model follows the pathways of water through dryland ecosystems, beginning with landscape attributes that affect water input, output and redistribution and ending with plant attributes that affect water extraction and use. We define vulnerability in the model as decreases in dominant native perennial plant species cover, an indicator of land degradation.

Like many dryland regions throughout the world, the Mojave Desert has heterogeneous landscape and soil attributes driven by complex topography and other factors of pedogenesis that strongly affect the spatial distribution and timing of plant-water availability (McAuliffe 1994; McDonald *et al.* 1996). Our model predicts that plants at higher elevations and on north-facing slopes are less vulnerable to reductions in perennial vegetation cover than low, south-facing landscape positions because they receive relatively high water input and experience lower evaporative losses (Shreve 1915). Perennial vegetation is likely buffered from decreases in cover along low-slope washes and playa margins due to periodic channel flow and run-on during storm events, whereas plants on alluvial fans and mountain slopes that experience run-off are more susceptible to warming and drying (Smith *et al.* 1995). Plants growing in soils with high sand content or low bulk density may be less vulnerable to elevated temperature and drought because high hydraulic conductivity allows water to percolate well below the surface, reducing evaporative losses and extending the rooting zone downwards (Noy-Meir 1973). Rock fragments at the surface can increase plant-water availability by limiting splash erosion, slowing sheetflow and decreasing evaporative losses (Poesen & Lavee 1994). The absence of restrictive subsurface layers (e.g. petrocalcic horizons), which is one characteristic of young geomorphic surfaces common throughout aridland systems, increases the potential for deep-root growth and water storage (McAuliffe 1994; Gibbens & Lenz 2001; Schwinning & Hooten 2009), thereby reducing the likelihood that shrub species in the Mojave Desert will succumb to warming and drying conditions.

Plant-water extraction and use depend on the life-history, structural and physiological attributes of each species (Smith, Monson & Anderson 1997; Hamerlynck *et al.* 2002; Schwinning & Hooten 2009). Long-lived evergreen species have drought-tolerant strategies and are less likely to lose cover than short-lived and deciduous species (Munson *et al.* 2013). Plant structural attributes, including deep roots and woody stem tissue coupled with physiological attributes, such as high water use efficiency (Ehleringer & Cooper 1988), and water-conserving photosynthetic pathways (Nobel 1991) can also help plant species resist elevated temperature and drought in the dryland ecosystems. Furthermore, the size-structure of plants often reflects their long-term adaptation to the hydrologic regime at a site, which can also influence their susceptibility to drought (McAuliffe & Hamerlynck 2010).

To improve our ability to predict the vulnerability of plant species to climate change and the potential for land degradation, there is a strong need to more explicitly consider the historical dynamic between climate and vegetation in the context of the aforementioned biological and physical attributes that affect water availability in dryland ecosystems. Our objectives are to (i) determine the responses of dominant plant species and functional types to changes in seasonal and annual climate variables and (ii) assess how these responses are mediated by biophysical attributes in our model. In order to address our objectives, we pair fifty years of repeated

Fig. 1. Conceptual model of the landscape, soil and plant attributes of dryland ecosystems and the hydraulic processes they influence that can increase plant vulnerability to elevated temperature and drought.

measures of plant species cover across the Mojave Desert with spatially explicit climate and soil models.

Materials and methods

The Mojave Desert supports plant assemblages dominated by evergreen and deciduous shrubs, which are well adapted to the uniseasonal precipitation regime. As is characteristic of the entire Mojave Desert (Hereford, Webb & Longpré 2006), most precipitation across our study sites occurs in the cool season of late fall to early spring (October–April [1960–2013] mean precipitation = 136 mm), when water demand through evapotranspiration is low, allowing water to percolate into the deep-rooting zone of shrub species. In contrast, the summer (July–September) at our study sites are extremely hot (mean max temperature = 34.1 °C), which creates high evaporative demand for limited precipitation (mean = 42 mm) and water stress for shallow-rooted species, including grasses. Despite low summer precipitation, there is a gradient of increasing summer water input from west to east in the Mojave Desert that is attributable to the North American Monsoon in July–September (Hereford, Webb & Longpré 2006). The distribution of plant-water availability is spatially heterogeneous, due to diverse topography and associated soil development of the Basin and Range physiographic province that includes the Mojave Desert (Hamerlynck *et al.* 2002).

DATA SYNTHESIS

We used repeated measurements of the cover of perennial species in permanently marked transects at six sites, which include 10 long-term studies in southern California and Nevada (Fig. 2, Table 1). Cover of annual species was excluded because of extremely high interannual variability, insufficient measurements and/or infrequent sampling intensity. The permanent plots we used range in elevation from 650 to 1730 m and include the margins of lowland playas and washes, upland benches and alluvial fans, and mountain slopes. Repeated measures of cover were made either using line or line-point intercepts along marked transects or by mapping canopy outlines of individual plants within a plot (chart quadrat). Measurements were taken in the spring (March–May) at intervals of 1–15 years (Table 1). Many of the sites had land-use effects that ranged from nuclear testing and military training exercises to livestock grazing; all sites have been protected from additional disturbances during the measurement period or we minimized their impacts by including only undisturbed plots.

Following the technique used by Blainey, Webb & Magirl (2007) for the Nevada National Security Site in southern Nevada, we extracted mean monthly temperature (minimum, mean, maximum) and precipitation from a climate model that integrates weather-station data from NOAA COOP (http://www.ncdc.noaa.gov), RAWs (http://www.raws.dri.edu) and station data collected by the Department of
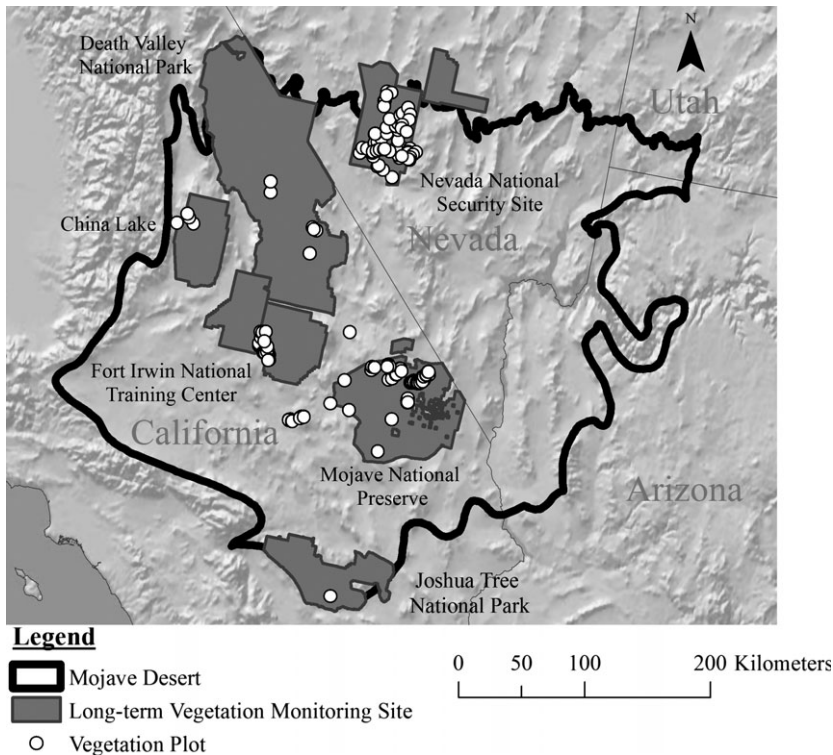
Fig. 2. Long-term vegetation monitoring sites and plots within the Mojave Desert.

Interior, Department of Defense and agricultural cooperatives (a total of 319 stations across the study region) with a 90-m digital-elevation model. Monthly temperature and precipitation data were spatially interpolated using a combination of multivariate regression of the geospatial position and inverse distance-square weighting, methods which outperform other standard geostatistical techniques, including kriging and co-kriging (Nalder & Wein 1998). Monthly climate variables were averaged over annual, winter (October–April) and summer (July–September) periods that preceded vegetation measurements at each plot.

We used the NRCS Gridded Soil Survey (gSSURGO) and State Soil (STATSGO) Geographic Databases (NRCS 2014) to extract soil attributes of each plot, including surface (top 15 cm) soil texture (% sand, silt and clay), small (% cover occupied by particles 2–74 mm in diameter) and large (> 74 mm in diameter) rock fragments in the surface soil, bulk density, depth to restrictive layer (a layer that significantly impedes the movement of water and root growth), and shallow (0–50 cm) and deep (> 50 cm) available water storage (the volume of water that the soil can store that is available to plants). We assumed that these generalized soils data were of sufficient resolution to characterize the physical setting of the permanent plots.

DATA ANALYSIS

We used non-metric multidimensional scaling and cluster analysis with plant species cover to delineate plant assemblages (PC-ORD 5.0, McCune & Mefford 2005). Species were subsequently aggregated into functional types according to forbs and grasses (herbaceous, non-woody plants), sub-shrubs (woody plants usually < 0.5 m and always < 1 m in height), shrubs (woody plants 1 4 m) and trees (woody plants > 4 m) (USDA 2014). For woody plants, we also distinguished between deciduous (due to winter or drought conditions) and evergreen species. Cover by species and aggregated by functional types was normalized across different sites and methods with a calculation of the change in cover per unit time:

$$\text{Change in cover} = \frac{\ln\left(\text{cover}_{t2}/\text{cover}_{t1}\right)}{t2 - t1} \qquad \text{eqn 1}$$

where cover$_{t2}$ is for year $t2$, and cover$_{t1}$ is for $t1$, the previous sampling year (Munson 2013). Positive values of this index indicate that a species had a net increase in cover between measurements, whereas negative values indicate a net decrease in cover.

We related climate, soil and landscape variables to the change in cover of species and functional types that had a suitable sample size greater than 20 repeated measurements across all sites. We first used zero-order correlations between the explanatory variables and change in cover to eliminate spurious variables that had correlations near zero (Murray & Conner 2009) and then used hierarchical partitioning, a multiple-regression technique that accounts for multicollinearity and shared power among explanatory variables better than comparable methods (Chevan & Sutherland 1991; 'hier.part' package in R, Walsh & Mac Nally 2009). To account for potential biotic interactions, we analysed species according to the assemblage type that they dominated; less abundant subdominant species were analysed across all assemblages. A total of fifteen change in cover values were identified as significant outliers using a Bonferroni Outlier Test ('car' package in R, Fox 2009) and removed from final analyses. We included the site where cover was measured in the model to account for variation in plant species cover related to site-specific attributes that we did not include in the analysis and differences in the way vegetation was measured across sites. In the cases when site was significant, we present results by site; otherwise, all sites are presented collectively.

Climate variables were averaged between vegetation sampling events, time intervals that are the same as those used in the change in cover index ($t2$–$t1$). We initially included climate variables representing

Table 1. Description (site, data set name, years measured, method, measurement units, objective of original measurement and reference) of long-term vegetation measurements

Long-term vegetation monitoring site	Data set	Years measured	Method	Measurement units	Objective of measurement	References
Mojave National Preserve	Globe-Hayden Fan Plots	2002, 2006, 2007	Chart Quadrat	8.0 × 50.0 m plots, 2 plots/site, 3 sites	Characterize plant-relevant soil water across a gradient of soil development	Nimmo *et al.* (2009)
Mojave National Preserve	Granite Mountains Plot	1981, 1996	Chart Quadrat	18.0 × 20.0 m plot, 1 plot/site, 1 site	Investigate survivorship and regeneration in desert plants	Cody (2000)
Mojave National Preserve	Desert Holly Plots	1992, 1997, 2002, 2007, 2012	Chart Quadrat	10.0 × 10.0 m plots, 6 plots/site, 2 sites	Document patterns of change in abundance, distribution, and gender expression	K. B. Hartney, unpubl. data
Mojave National Preserve	Livestock Exclosure Plots	2001–2003, 2009–2010	Line-point intercept	50 m transects (50 points/transect), 9 transects/site, 15 sites	Understand the effects of livestock removal according to historic grazing intensity.	Beever, Huso & Pyke (2006)
Mojave National Preserve	Clim-Met Station	2000–2011	Line intercept	100 m transect, 1 transect/site, 3 sites	Understand Southwest vegetation distribution in terms of climate, substrate, and wind erosion vulnerability	Belnap *et al.* (2009)
Death Valley National Park	Ghost Town Plots	1979–1985, 1998–1999	Line intercept	400 m transects, 1 transect/site, 10 sites	Determine recovery rate of vegetation and soil in a former town site	Webb & Wilshire (1980)
Nevada National Security Site	Beatley Plots	1963–1967, 1970, 1975, 1989, 1999–2003, 2005, 2011	Line intercept	30 × 30 m plots, 1 plot/site, 68 sites	Describe and map plant communities, address long-term dynamics	Beatley (1974a,b, 1980)
Fort Irwin National Training Center	Integrated Training Area Management (ITAM) Plots	1993, 2001, 2005, 2009, 2012	Line intercept	100 m transects, 1 transect/site, 21 sites	Monitor habitat for military training	D. C. Housman, unpubl. data
China Lake	Coso Grazing Exclosure Plots	1988–1989, 1994, 2005–2007	Line intercept, Ocular estimate	25 m transects, 10 transects/site, 4 sites	Describe Mohave ground squirrel habitat	Leitner & Leitner (1998)
Joshua Tree National Park	Permanent Study Plot	1984, 1989, 1994, 1999, 2000, 2004	Chart Quadrat	100.0 × 100.0 m plot, 1 plot/site, 1 site	Understand the spatiotemporal dynamics in a desert perennial community	Miriti *et al.* (2007)

12, 24 and 60 months before vegetation measurements to account for the lags and cumulative impacts of climate at different time scales; these additional variables did not improve model fits and were not retained in the analysis. Maximum and minimum temperatures, in addition to elevation, were also excluded because they were highly correlated with mean temperatures. To determine whether extending the time interval between vegetation measurements and averaging over years of associated climate would lead to any biases in the climate–plant relationship, we compiled all the data on *Larrea tridentata* (the species with the highest cover in our data set) measured on an annual basis and averaged winter precipitation and change in cover by 2-year, 5-year and 10-year intervals. We found that extending the interval did not significantly change the precipitation – *Larrea* relationship (ANCOVA winter precipitation × time interval interaction: $F = 0.004$, $P = 0.94$). We also included the year of the vegetation measurement as a potential correlate to determine whether there were inter-annual changes in cover not explained by the climate variables.

We used the slope of the regression line between change in cover of a species or functional type and the climate variable (multiplied by 1000) to define a 'plant response'. The x-intercept point, where the regression line intersects the x-axis, is the 'climate pivot point' (Munson 2013) representing the climate variable at which no change in cover occurs, and there is a transition between increases and decreases in cover. We include standard errors in both our estimates of plant response and climate pivot points to address uncertainty. For species that had a change in cover explained by both climate and soil properties, we examined how plant responses and climate pivot points were modified by the soil variables using plots where more than five repeat measurements were taken (to estimate regression slope and pivot point with more precision). We also determined the responses and climate pivot points of plant functional types by summing cover of all species within a functional type. In the cases when site interacted with a climate variable, as determined by ANCOVA, we present the response and pivot point according to site.

Results

We identified four types of plant assemblages in the permanent plot data using cluster analysis and NMDS. These plant

assemblages included (i) *Larrea tridentata* – dominated assemblages (*Larrea tridentata* – *Ambrosia dumosa*; *Larrea tridentata* – *Grayia spinosa* – *Lycium andersonii*; *Larrea tridentata* – *Coleogyne ramosissima*; *Larrea tridentata* – *Acacia greggii*), (ii) *Grayia spinosa* – *Lycium andersonii* – dominated assemblages, (iii) *Coleogyne ramosissima* – dominated assemblages and (iv) *Atriplex* spp. – dominated assemblages.

Climate, soil and landscape attributes; site; and time explained 11–58% of the variation in the change in cover of dominant plant species and functional types (Table 2). Annual and seasonal precipitation were positively related to changes in cover of all perennial vegetation and many dominant species. Winter precipitation best explained changes in cover of the evergreen shrubs *Larrea tridentata* and *Grayia spinosa*, whereas summer precipitation was more important in explaining changes in cover of the deciduous sub-shrub *Ambrosia dumosa* (Fig. 3a–c). For some species, including *Larrea* and *Ambrosia*, the responses and climate pivot points varied significantly by site (*Larrea*: $F_{6,229} = 4.47$, $P = 0.0003$; *Ambrosia*: $F_{4,211} = 3.06$, $P = 0.02$); for others, including *Grayia*, these indices were the same across sites ($F_{3,81} = 1.05$, $P = 0.36$). For example, *Larrea* had a lower response at Fort Irwin (slope of 0.67 ± 0.28) compared to the LivestockEx site in the Mojave National Preserve (1.73 ± 0.50; $t = 2.02$, $P = 0.04$). *Larrea* at the ClimMet site in the Mojave National Preserve had a lower winter precipitation pivot point (55 ± 20 mm) than both Fort Irwin (175 ± 21 mm; $t = 2.38$, $P = 0.02$) and the LivestockEx site (151 ± 18 mm; $t = 2.98$, $P = 0.001$). *Larrea* at all other sites had no significant relationship with winter precipitation.

Annual and seasonal temperatures were negatively related to changes in cover of *Larrea*, *Ambrosia* and *Krameria* as well as the deciduous shrubs *Lycium andersonii* (Fig. 3d) and *Hymenoclea salsola*. Some of the plant species that had significant responses to temperature also had significant changes in time, and it was not always possible to distinguish between the influences of these covarying factors (Table 2). One exception was *Achnatherum hymenoides*, a common C_3 perennial grass, which decreased through time but not with increasing temperatures.

While plant functional types were responsive to different seasons of precipitation, most were sensitive to annual precipitation, which provided a comparison of their responses and climate pivot points. Evergreen shrubs had the lowest responses (slope of 0.25 ± 0.07) and pivot points (x-intercept of 161 ± 18 mm) with respect to annual precipitation (Fig. 4), C_3 perennial grasses had higher responses (1.51 ± 0.42; $t = 3.01$, $P = 0.003$) and pivot points (203 ± 21 mm; $t = 1.71$, $P = 0.04$), and deciduous shrubs and sub-shrubs had intermediate responses and pivot points. Similarly, all herbaceous perennial vegetation had higher responses (1.63 ± 0.47) than woody vegetation (0.34 ± 0.07; $t = 3.91$, $P = 0.0001$), but there was overlap in their annual precipitation pivot points (200 ± 16 mm and 186 ± 13 mm, respectively; $t = 0.77$, $P = 0.44$).

Whereas climate had the most important influence on changes in plant species cover overall, landscape and soil attributes also affected changes in cover, as predicted by our model. Topographic slope was negatively related to change in cover of *Atriplex polycarpa* and *Ephedra nevadensis* and positively related to *Hymenoclea salsola*, whereas slope explained higher perennial forb responses on south and west compared to north-facing aspects. Coarse-textured soil (sand >70%) had a positive influence, and fine-textured soil (silt + clay >30%) had a negative influence on all perennial vegetation, *Larrea* and evergreen shrubs. Conversely, coarse-textured soil had a negative influence and fine-textured soil a positive influence on *Ambrosia* and deciduous sub-shrubs, *Atriplex confertifolia*, evergreen sub-shrubs and cacti. Surface soils with high cover of small (>30%) and large (>4%) rock fragments were positively related to changes in cover of deciduous (*Ambrosia*) and evergreen (*Atriplex confertifolia*) sub-shrubs, respectively, but small rock fragments were negatively associated with changes in abundance of cacti. Change in cover of *Ambrosia*, *Ephedra* and all sub-shrub species were negatively related to increasing depth to restrictive layer. Change in cover of *Coleogyne ramosissima*, a dominant evergreen shrub, was negatively related to increasing bulk density.

The responses and pivot points of dominant plant species were modified by soil attributes. The response of *Larrea* to winter precipitation in plots that were repeatedly measured a minimum of five times (to estimate the slope with more precision) decreased 84% as sand content increased from 60 to 80% ($r^2 = 0.28$, $P < 0.01$; Fig. 5a). There was no significant relationship between the winter-precipitation pivot point of this evergreen shrub and soil texture. In contrast, the summer-precipitation pivot point of *Ambrosia* significantly decreased with increasing clay content ($r^2 = 0.24$, $P = 0.04$; Fig. 5b), but responses to summer precipitation were not modified by soil texture.

Discussion

Our results demonstrate the impacts of climate on the cover of dominant perennial plants across the Mojave Desert over the last fifty years, and how landscape, soil and plant attributes in our conceptual model can mediate these changes. Drought- and elevated temperature-induced impacts, in particular, can serve as an important indicator of how plant assemblages may shift in a region that is projected to become increasingly arid. The loss of plant cover beyond climate pivot points represents vulnerability because there is reduced capacity for growth, survival and reproduction. These reductions may be reversible as climatic conditions become favourable, and many desert plants can survive if only increasing in rare years that make up for many years of slow decline (Cody 2000). Reductions in cover of plant species may also be compensated for by other species in the area. However, extreme or sustained climatic conditions beyond pivot points of multiple dominant species can lead to permanent and irreversible alteration of dryland ecosystems (Munson 2013).

Plant species varied in sensitivity to different aspects of climate, which is partially attributable to their structural and

Table 2. The independent effects (% of R^2) of annual and seasonal precipitation (mm) and temperature (°C), landscape (slope and aspect) and soil attributes (texture, rock fragments, bulk density, depth to restrictive layer, available water storage), time (year) and site to explain change in plant species and functional type canopy cover as determined by hierarchical partitioning. Bold values represent positive effects, (values in parentheses) represent negative effects, and blank cells are not significant. The R^2, P and N values represent test results for the full model of all effects. Only effects found to be significant ($P < 0.05$) by zero-order correlations were included in the full model

Plant species / Functional type	Climate: Precipitation			Temperature			Landscape		Soil: Texture			Rock Fragments		Bulk Density	Depth to Restrictive Layer	Available Water Storage		Year	Site	R^2	P	N
	Annual	Winter	Summer	Annual	Winter	Summer	Slope	Aspect	Sand	Clay	Silt	Small	Large			Shallow	Deep					
Larrea dominated																						
Larrea tridentata	**20.64**	**24.09**		(14.25)	(13.30)				**7.56**		(6.40)									**13.76**	0.35	0.0000	235
Ambrosia dumosa	**16.16**		**30.90**	(10.36)						**12.00**			**13.80**		(7.27)				**9.51**	0.58	0.0000	216
Coleogyne dominated																						
Coleogyne ramosissima														(31.75)			(19.60)		**48.65**	0.27	0.0076	50
Grayia-Lycium dominated																						
Grayia spinosa	**36.78**	**63.22**																		0.24	0.0006	85
Lycium andersonii				(40.06)	(17.45)	(25.00)												(17.49)		0.40	0.0000	70
Atriplex dominated																						
Atriplex hymenelytra				(100.00)																0.38	0.0009	48
Atriplex polycarpa				**20.39**			(43.12)											**36.49**		0.23	0.0281	37
Atriplex confertifolia										**15.32**		**23.48**				(16.44)		(23.45)	**21.31**	0.27	0.0412	38
All Communities																						
Ephedra nevadensis	(35.49)	(34.01)		(30.50)																0.10	0.0342	168
Krameria erecta	**34.45**		**28.13**															(37.42)		0.14	0.0369	59
Krascheninnikovia lanata							(22.00)			(17.88)					(15.70)				**44.42**	0.12	0.0015	51
Achnatherum hymenoides																		(100.00)		0.14	0.0001	106
Hymenoclea salsola				(22.35)	(15.85)	(17.70)	**14.69**											(29.41)		0.22	0.0401	54
Acamptopappus shockleyi		**54.42**													**45.58**					0.13	0.0096	68
Lycium pallidum	**27.22**		**72.78**																	0.45	0.0018	24
Cacti									(18.73)		**26.66**	(21.90)							**32.71**	0.31	0.0067	63
Deciduous Shrubs	**23.31**	**16.09**	**9.00**	(11.80)	(14.81)														**24.97**	0.13	0.0074	243
Deciduous Subshrubs	**18.12**	**15.63**	**20.42**	(5.18)	(6.03)					**6.43**					(5.28)			(5.30)	**17.61**	0.36	0.0000	232
Evergreen Shrubs	**16.59**	**14.82**		(7.84)	(7.23)				**13.90**	**7.10**									**32.01**	0.18	0.0000	385
Evergreen Subshrubs										(10.82)	(11.86)	**8.27**	**9.45**		(18.52)			(19.67)	**21.92**	0.16	0.0092	233
All Woody Vegetation	**21.39**	**16.42**	**7.32**						**8.06**		(8.21)								**38.60**	0.23	0.0000	396
C3 Perennial Grasses	**27.29**	**29.64**																	**43.07**	0.11	0.0127	156
C4 Perennial Grasses	**18.72**		**63.82**	(17.46)																0.23	0.0917	27
Perennial Forbs	**27.36**	**28.26**						**44.38**												0.08	0.1038	94
All Perennial	**32.78**	**25.87**	**18.27**																**23.08**	0.16	0.0021	186
Herbaceous Vegetation																						
All Perennial Vegetation	**26.53**	**22.54**							**9.71**		(9.75)								**31.47**	0.15	0.0000	436
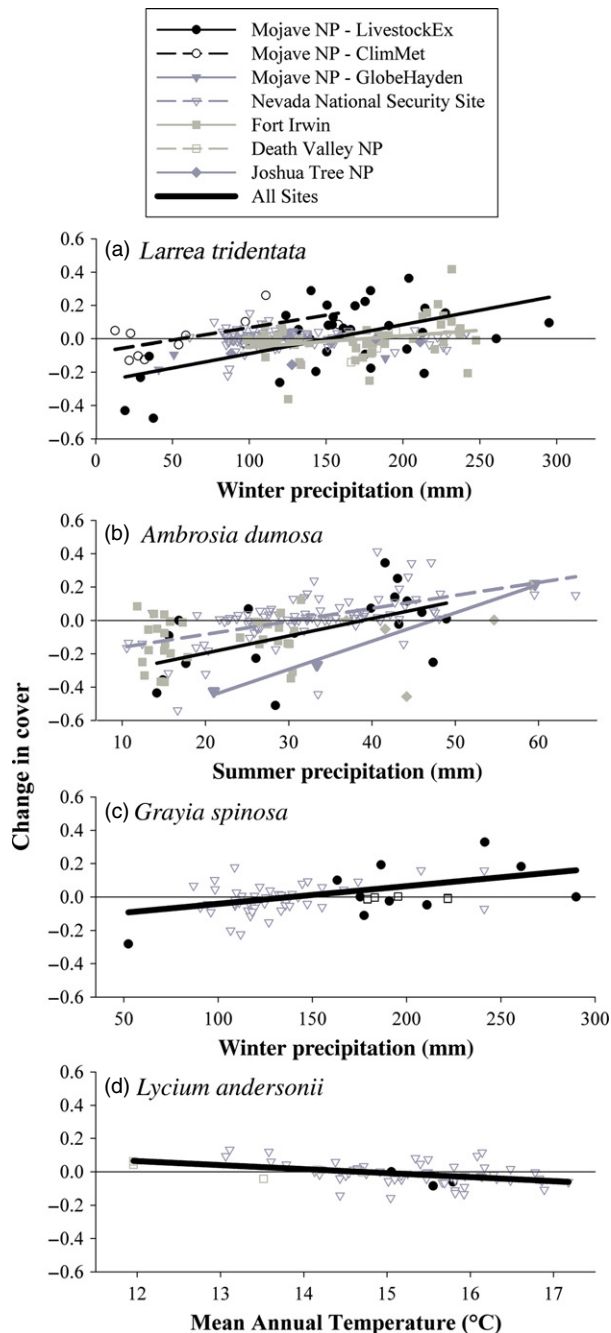
Fig. 3. Change in cover of dominant species *Larrea tridentata* (a), *Ambrosia dumosa* (b), *Grayia spinosa* (c) and *Lycium andersonii* (d) in relation to climate variables across sites in the Mojave Desert. NP = National Park. Significant linear regressions are represented by lines for *Larrea* at the sites: Mojave NP – LivestockEx ($y = 0.002x - 0.26$, $r^2 = 0.29$, $P = 0.002$); Mojave NP – ClimMet ($y = 0.002x - 0.08$, $r^2 = 0.36$, $P = 0.04$); Fort Irwin ($y = 0.001x - 0.12$, $r^2 = 0.09$, $P = 0.02$). Significant linear regressions for *Ambrosia* at the sites: Mojave NP – LivestockEx ($y = 0.010x - 0.40$, $r^2 = 0.32$, $P = 0.014$); Nevada National Security Site ($y = 0.008x - 0.24$, $r^2 = 0.31$, $P < 0.0001$); Joshua Tree NP ($y = 0.017x - 0.80$, $r^2 = 0.98$, $P = 0.04$). Significant linear regressions for *Grayia* ($y = 0.001x - 0.14$, $r^2 = 0.19$, $P = 0.0003$) and *Lycium* ($y = -0.024x + 0.35$, $r^2 = 0.19$, $P = 0.0002$) across all sites (no significant site effect).
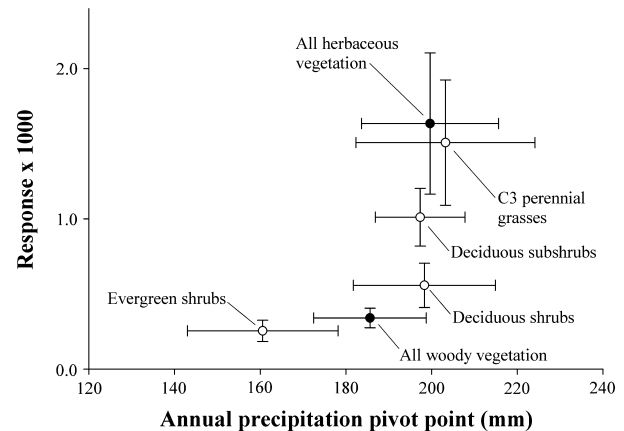
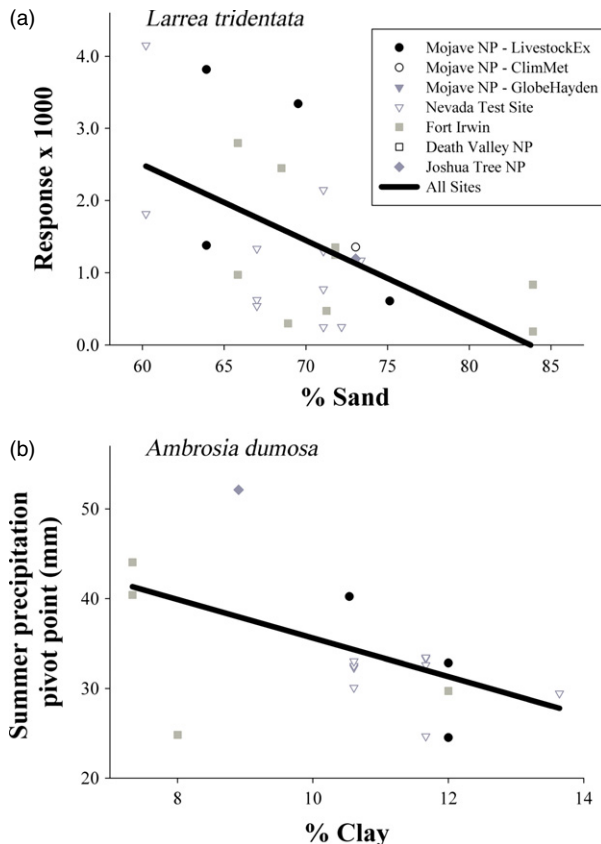Fig. 4. Response (change in cover mm^{-1} year^{-1}) ($\pm$SE) of plant functional types (unfilled points), all herbaceous and woody vegetation (filled points) in relation to annual precipitation pivot point (mm) ($\pm$SE). Low annual precipitation pivot points indicate high drought resistance.

physiological traits. Changes in the abundance of evergreen shrubs were primarily related to winter precipitation when evaporation is low and deep-water percolation occurs. Changes in the cover of deciduous woody species were driven by precipitation throughout the year, including the summer. This sensitivity of drought-deciduous species to summer precipitation, including *Ambrosia* and *Lycium pallidum*, is due to leaf retention into warmer months if there is adequate soil moisture, which prolongs growth, or leaf drop if there is limited water supply into the summer (Bamberg *et al.* 1975). Our result of differences among woody species in their use of summer precipitation has been previously shown in the Mojave and adjacent deserts (Ehleringer *et al.* 1991), and it forecasts their relative responses as the magnitude and timing of the North American Monsoon changes in the future (Lee & Wang 2014).

Cool-season precipitation was also an important driver for C$_3$ perennial grasses and forbs. While species represented by these plant functional types generally do not have high abundance (<10% cover), many can overwinter after producing new vegetative parts in response to fall precipitation or rapidly grow following heavy winter and spring precipitation (Beatley 1974a). In contrast to C$_3$ perennial grasses, the changes in cover of C$_4$ perennial grasses were better explained by summer precipitation, which fits general patterns of seasonal water use among herbaceous vegetation with these different photosynthetic pathways (Ehleringer 2005).

High temperatures negatively affected the cover of each of several species on its own (*Lycium andersonii*, *Hymenoclea salsola*) and in combination with low precipitation for other species (*Larrea*, *Ambrosia*). Heat stress can decrease photosynthetic rates, stomatal conductance and recovery rates of *Larrea tridentata*, but only when this evergreen shrub is already subjected to drought (Hamerlynck *et al.* 2000). Perhaps more important than direct effects to vegetation, high

Fig. 5. Response (change in cover mm^{-1} year^{-1}) of *Larrea tridentata* to winter precipitation in relation to % sand content (a) and summer-precipitation pivot point of *Ambrosia dumosa* in relation to % clay content (b) at each plot or transect. *Larrea* linear regression: y = −0.10x + 8.6, r^2 = 0.28, P < 0.01; *Ambrosia* linear regression: y = −2.2x + 57, r^2 = 0.24, P = 0.04.

temperatures modify water availability through increased evaporation. Changes in CO_2 over the 50-year study period may have also influenced changes in perennial vegetation cover, as increases of this greenhouse gas have experimentally been shown to induce stomatal closure and increase soil-water availability in grasslands and semi-arid ecosystems (Morgan *et al.* 2004). However, soil water was not conserved in the more arid Mojave Desert under experimental increases in CO_2 because marginal water input for plant growth overwhelms the CO_2 effect (Nowak *et al.* 2004).

Plant attributes in our model helped clarify species responses to drought. There was a strong contrast between evergreen shrubs that had low climate pivot points and responses with respect to annual precipitation and C$_3$ perennial grasses and deciduous sub-shrubs that had high climate pivot points and responses. The low precipitation pivot point of evergreen shrubs means that they are able to maintain increases in cover at low amounts of water input and therefore indicates high drought resistance, whereas the low response indicates this functional type has small losses and gains in cover as water availability changes. In contrast, C3 perennial grasses and deciduous sub-shrubs had low drought resistance and a high potential to change in cover with shifts

from dry to wet conditions. The divergence in responses and climate pivot points among plant functional types demonstrates a trade-off between the ability of a plant to respond to abundant resources and tolerate resource shortages (Parsons 1968; Grime 1979). In deserts, plant strategies to cope with drought include either fluctuating between large growth responses following wet periods and senescence in dry periods, or increasing water-use efficiency to withstand drought and slow growth rates (Parsons 1968). The primary reason for this trade-off is that opening stomata to increase carbon dioxide intake also increases water loss, and therefore, plants cannot maximize carbon gain or minimize water loss without a cost. Plant investment in woody tissue can also come at a cost of limited ability to respond to precipitation, as there was a difference in responses between woody and herbaceous vegetation. The higher climate pivot point in deciduous relative to evergreen shrubs was likely due to decreases in cover explained by leaf drop.

Landscape attributes in our model partially explained plant vulnerability to elevated temperature and drought. The high response and low winter-precipitation pivot point of *Larrea* at the Mojave-ClimMet site relative to the other sites could be because the shrub species is near a playa along the intermittent Mojave River where run-on from higher elevations and distributary flow during floods can supplement water and promote increases in cover even if there is low precipitation at the site. Water redistribution may also explain why *Atriplex polycarpa* had greater increases in cover in low-slope landscape positions relative to sites with higher slopes. It is possible that plant species with different responses across sites and landscape positions represent locally adapted 'ecotypes', especially given the high degree of polyploidy and associated reproductive isolation in desert shrubs like *Larrea* and *Ambrosia* (Hunter *et al.* 2001). An overall lack of relationship between *Larrea* and cool-season precipitation at the Nevada National Security Site was unexpected given past documentation of the importance of precipitation (Beatley 1974b). Although the change in cover of *Larrea* in some plots was related to cool-season precipitation, many plots did not have a relationship because of surface-water redistribution, which causes lower than expected cover.

Our model shows that the vulnerability of plant species to elevated temperature and drought was mediated by soil attributes that likely affected water infiltration, permeability and water-holding capacity (McDonald *et al.* 1996). Soils high in sand and low in clay and silt contents were associated with increases in the cover of evergreen shrubs, including *Larrea tridentata*. While soil properties can affect plant growth through many mechanisms (e.g. nutrient availability, substrate), their influence through effects on water availability is supported because increasing sand content resulted in a lower response of *Larrea* to winter precipitation. Our results based on long-term monitoring indicate that the most abundant shrub in the Mojave Desert is buffered from losses when it occurs on soils with high sand content. Observations of *Larrea* distribution, abundance and physiology across soil gradients have long supported improved performance of the

evergreen shrub on soils that allow for rapid and deep movement of water and root aeration (Shreve & Wiggins 1964; Burk & Dick-Peddie 1973; McAuliffe 1994). Soil characteristics can also affect the size-structure of *Larrea* plants (Hamerlynck *et al.* 2002), which in turn can affect their relative susceptibility to decline or mortality (McAuliffe & Hamerlynck 2010).

In contrast to the negative effect of fine-textured soils on *Larrea*, soils with high clay and silt were positively associated with increases in cover of shallow-rooted woody species, including *Ambrosia dumosa*, *Atriplex confertifolia*, in addition to evergreen sub-shrubs and cacti. Soils with high clay-silt content have high water retention near the surface, which is advantageous to plants with roots in the upper soil horizons (Young *et al.* 2004). Similar to *Larrea*, soil properties interacted with precipitation to affect the performance of *Ambrosia*. This drought-deciduous sub-shrub had a decrease in its pivot point response to summer precipitation with increase in clay content. In other words, losses in *Ambrosia* cover occurred at a very low amount of water input on soils with relatively high clay content, suggesting that the shrub is more likely to retain leaves and be photosynthetically active into the summer months if it occurs on soils where water retention is high near the surface. Change in *Ambrosia* cover was also sensitive to annual precipitation, and many very dry summers were preceded by low precipitation early in the growing season. Improved performance of *Ambrosia* on fine-textured soils is supported by previous results because its total canopy volume was high and its physiological performance unaffected on soils with limited capacity for water percolation relative to well-drained soils (Hamerlynck *et al.* 2002). For *Atriplex*, a halophyte, the increase in cover with high clay may also be explained by the higher salinity associated with fine-grained soils (Branson, Miller & McQueen 1967).

Shallow-rooted woody species and functional types were more likely to increase in cover when they occurred on soils with a high amount of rock fragments in the surface and shallow restrictive layers. Rock fragments may have influenced the performance of shallow-rooted species by slowing sheetflow or dampening the effect of evaporative water loss (Poesen & Lavee 1994). Very small rock fragments associated with fine-grained Av horizons that comprise desert pavement most likely had a negative effect on the change in abundance of cacti because they can limit infiltration and increase run-off (Wood, Graham & Wells 2005). Shallow-rooted species had a shift from increases to decreases in cover as the depth to restrictive layers increased. Like soils high in clay and silt, a shallow restrictive layer can keep upper soil layers wet by preventing water from deep percolation, which makes water more accessible to plants with shallow roots. Shallow-rooted species may also benefit from hydraulic redistribution of water towards the surface by deep-rooted species (Neumann & Cardon 2012).

We acknowledge that the spatial models of soils that we used for this study (gSSURGO, STATSGO) have limitations. In particular, this polygon-organized data may insufficiently address spatial variability that might provide more meaningful assessments of site-level infiltration properties and the spatial extent of restrictive soil layers that may have increased our explanatory power. We were unable to characterize the soil profile at each site, in part due to restrictions on soil sampling inside parks and at sites where previous nuclear tests had been conducted (Nevada National Security Site). However, the clear overall patterns that emerged in our results show that this characterization was sufficient to reveal a role of soils in mediating long-term changes in the cover of perennial plant species. There was a substantial amount of variation in the change in cover of plant species that was not explained by climate, landscape, soil and plant attributes. Plant responses can also be related to short-term climatic events (e.g. extreme freeze), lags in climatic conditions, historical land-use impacts and plot-level characteristics including biotic interactions, invasive non-native annual species and nutrient availability, which we were not able to entirely account for in this study. Furthermore, plant responses may be dependent on demography and size-structure, genotype, reproductive output and other factors that could not be assessed by looking at changes in cover alone.

Despite the longevity and slow growth of many perennial plants in the Mojave Desert, our results reveal that long-term changes in the timing and amount of precipitation coupled with increases in temperature can drive shifts in the cover of woody and herbaceous species. These climate impacts serve as an important indicator of how plant assemblages and ecosystems may shift as the region is projected to become increasingly arid. Our model of plant vulnerability to elevated temperature and drought was a useful framework to test previous research findings with our long-term results, leading to an integrated understanding of how biophysical attributes can influence water availability in dryland ecosystems. We view this model as a starting point to expand beyond climate predictions and bioclimate envelope models, which rely on the assumption of current climate-vegetation equilibrium and often ignore important determinants of ecosystem water balance (Araújo & Peterson 2012). Although there are exceptions to the general patterns highlighted in the model, this framework provides an important means to further test how plant species responses to climate are moderated by biophysical traits. Importantly, our assessment of the vulnerability of perennial plant species to elevated temperature and drought indicates the potential for land degradation, marked by detrimental shifts to ecosystem condition (UNCCD 1994; MEA 2005). Declines in productive capacity, soil surface protection from erosion and functional wildlife habitat may result from decreases in perennial vegetation cover as the southwestern United States, and dry lands globally are expected to face more severe water limitations.

Acknowledgements

Author contributions

S.M.M. conceived the project, analysed data and led writing of the paper with R.H.W., who also contributed data; D.C.H., K.E.V. and E.A.B. co-wrote the paper and contributed data; K.E.N. developed the climate model; and all other co-authors contributed data. The authors have no conflict of interest to declare. Any use of trade, product or firm names in this article is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Data accessibility

Data used in this study are archived by the U.S. Geological Survey: http://www.werc.usgs.gov/ProductDetails.aspx?ID=2780, http://gec.cr.usgs.gov/projects/sw/clim-met; and additional data can be accessed from references in Table 1.

References

Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527–1539.

Bamberg, S.A., Kleinkopf, G.E., Wallace, A. & Vollmer, A. (1975) Comparative photosynthetic production of Mojave Desert shrubs. *Ecology*, **56**, 732–736.

Beatley, J.C. (1974a) Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology*, **55**, 856–863.

Beatley, J.C. (1974b) Effects of rainfall and temperature on the distribution and behavior of *Larrea tridentata* (creosote-bush) in the Mojave Desert of Nevada. *Ecology*, **55**, 245–261.

Beatley, J.C. (1980) Fluctuations and stability in climax shrub and woodland vegetation of the Mojave, Great Basin and Transition Deserts of southern Nevada. *Israel Journal of Botany*, **28**, 149–168.

Beever, E.A., Huso, M. & Pyke, D.A. (2006) Multiscale responses of soil stability and invasive plants to removal of non-native grazers from an arid conservation reserve. *Diversity and Distributions*, **12**, 258–268.

Belnap, J., Reynolds, R.L., Reheis, M.C., Phillips, S.L., Urban, F.E. & Goldstein, H.L. (2009) Sediment losses and gains across a gradient of livestock grazing and plant invasion in a cool, semi-arid grassland, Colorado Plateau, USA. *Aeolian Research*, **1**, 27–43.

Blainey, J., Webb, R. & Magirl, C. (2007) Modeling the spatial and temporal variation of monthly and seasonal precipitation on the Nevada Test Site, 1960-2006: U.S. Geological Survey Open-file Report 2007–1269. available at http://pubs.usgs.gov/of/2007/1269.

Branson, F.A., Miller, R.F. & McQueen, I.S. (1967) Geographic distribution and factors affecting the distribution of salt desert shrubs in the United States. *Journal of Range Management*, **20**, 287–296.

Burk, J.H. & Dick-Peddie, W.A. (1973) Comparative production of *Larrea divaricata* Cav. on three geomorphic surfaces in southern New Mexico. *Ecology*, **54**, 1094–1102.

Cayan, D.R., Das, T., Pierce, D.W., Barnett, T.P., Tyree, M. & Gershunov, A. (2010) Future dryness in the southwest US and the hydrology of the 21st century drought. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21271–21276.

Cayan, D., Tyree, M., Kunkel, K.E., Castro, C., Gershunov, A., Barsugli, J. *et al.* (2013) Future Climate: Projected Average. *Assessment of Climate Change in the Southwest United States: A Report Prepared for the National Climate Assessment* (eds G. Garfin, A. Jardine, R. Merideth, M. Black & S. LeRoy), pp. 101–125. Island Press, Washington, DC.

Chevan, A. & Sutherland, M. (1991) Hierarchical partitioning. *American Statistician*, **45**, 90–96.

Cody, M.L. (2000) Slow-motion population dynamics in Mojave Desert perennial plants. *Journal of Vegetation Science*, **11**, 351–358.

Cole, K.L. & Webb, R.H. (1985) Late Holocene changes in Greenwater Valley, Mojave Desert, California. *Quaternary Research*, **23**, 227–235.

Ehleringer, J.R. (2005) The influence of CO_2, temperature, and water on the abundance of C_3/C_4 taxa. *A History of Atmospheric CO2 and its Effects on Plants, Animals, and Ecosystems* (eds J.R. Ehleringer, T. Cerling & M.D. Dearing), pp. 214–231. Springer, New York.

Ehleringer, J.R. & Cooper, T.A. (1988) Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia*, **76**, 562–566.

Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F. & Sandquist, D.R. (1991) Differential utilization of summer rains by desert plants. *Oecologia*, **88**, 430–434.

Fox, J. (2009) car: companion to applied regression. R package version 1.2-16.

Gibbens, R.P. & Lenz, J.M. (2001) Root systems of some Chihuahuan Desert plants. *Journal of Arid Environments*, **49**, 221–263.

Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. Wiley and Sons, Chichester, UK.

Hamerlynck, E.P., Huxman, T.E., Loik, M.E. & Smith, S.D. (2000) Effects of extreme high temperature, drought, and elevated CO_2 on photosynthesis of the Mojave Desert evergreen shrub, *Larrea tridentata*. *Plant Ecology*, **148**, 183–193.

Hamerlynck, E.P., McAuliffe, J.R., McDonald, E.V. & Smith, S.D. (2002) Ecological response of two Mojave Desert shrubs to soil horizon development and soil water dynamics. *Ecology*, **83**, 768–779.

Hereford, R., Webb, R.H. & Longpré, C.I. (2006) Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave Desert region, 1893-2001. *Journal of Arid Environments*, **67**, 13–64.

Hunter, K.L., Betancourt, J.L., Riddle, B.R., Van Devenender, T.R., Cole, K.L. & Spaulding, W.G. (2001) Ploidy race distributions since the last glacial maximum in the North American desert shrub, *Larrea tridentata*. *Global Ecology & Biogeography*, **10**, 521–533.

Intergovernmental Panel on Climate Change (IPCC) (2013). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group 1 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds T.F. Stocker, D. Qin, G.K. Plattner, M.M.B. Tignor *et al.*), Cambridge University Press, Cambridge.

Lee, J. & Wang, B. (2014) Future change in global monsoon in the CMIP5. *Climate Dynamics*, **42**, 101–119.

Leitner, P. & Leitner, B. (1998) *Coso Grazing Exclosure Monitoring Study: Mohave Ground Squirrel Study*. CalEnergy Company Inc, Orinda, CA.

McAuliffe, J.R. (1994) Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. *Ecological Monographs*, **64**, 112–148.

McAuliffe, J.R. & Hamerlynck, E.P. (2010) Perennial plant mortality in the Sonoran and Mojave deserts in response to severe, multi-year drought. *Journal of Arid Environments*, **74**, 885–896.

McCune, B. & Mefford, M.J. (2005) *PC-ORD. Multivariate Analysis of Ecological Data. Version 5.0 MjM Software*. Gleneden Beach, Oregon.

McDonald, E.V., Pierson, F.B., Flerchinger, G.N. & McFadden, L.D. (1996) Application of a soil-water balance model to evaluate the influence of Holocene climate change on calcic soils, Mojave Desert, California, USA. *Geoderma*, **74**, 167–192.

Millennium Ecosystem Assessment (MEA) (2005) *Ecosystems and Human Well-Being: Desertification Synthesis*. World Resources Institute, Washington, DC.

Miriti, M.N., Rodriguez-Buritica, S., Wright, S.J. & Howe, H.F. (2007) Episodic death across species of desert shrubs. *Ecology*, **88**, 32–36.

Morgan, J.A., Pataki, D.E., Körner, C., Clark, H., Del Grosso, S.J., Grünzweig, J.M. *et al.* (2004) Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. *Oecologia*, **140**, 11–25.

Munson, S.M. (2013) Plant responses, climate pivot points, and tradeoffs in water-limited ecosystems. *Ecosphere*, **4**, Art 109.

Munson, S.M., Belnap, J. & Okin, G.S. (2011) Responses of wind erosion to climate induced vegetation changes on the Colorado Plateau. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 3854–3859.

Munson, S.M., Muldavin, E.H., Belnap, J., Peters, D.P.C., Anderson, J.P., Reiser, M.H., Gallo, K., Melgoza, A., Herrick, J.E. & Christiansen, T.A. (2013) Regional signatures of plant response to drought and elevated temperature across a desert ecosystem. *Ecology*, **94**, 2030–2041.

Murray, K. & Conner, M.M. (2009) Methods to quantify variable importance: implications for the analysis of noisy ecological data. *Ecology*, **90**, 348–355.

Nalder, I. & Wein, R. (1998) Spatial interpolation of climatic normals: test of a new method in the Canadian boreal forest. *Agricultural and Forest Meteorology*, **92**, 211–225.

Natural Resources Conservation Service (NRCS) (2014) Web Soil Survey. available at http://websoilsurvey.nrcs.usda.gov Accessed January 3, 2014.

Neumann, R.B. & Cardon, Z.G. (2012) The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. *New Phytologist*, **194**, 337–352.

Nimmo, J.R., Perkins, K.S., Schmidt, K.M., Miller, D.M., Stock, J.D. & Singha, K. (2009) Hydrologic characterization of desert soils with varying degrees of pedogenesis. *Vadose Zone*, **8**, 480–495.

Nobel, P.S. (1991) Achievable productivities of certain CAM plants: basis for high values compared with C_3 and C_4 plants. *New Phytologist*, **119**, 183–205.

Nowak, R.S., Zitzer, S.F., Babcock, D., Smith-Longozo, V., Charlet, T.N., Coleman, J.S., Seemann, J.R. & Smith, S.D. (2004) Elevated atmospheric CO2 does not conserve soil water in the Mojave Desert. *Ecology*, **85**, 93–99.

Noy-Meir, I. (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**, 23–51.

Parsons, R.F. (1968) The significance of growth-rate comparisons for plant ecology. *American Midland Naturalist*, **102**, 595–597.

Poesen, J.W. & Lavee, H. (1994) Rock fragments in top soils: significance and processes. *Catena*, **23**, 1–28.

Ratajczak, Z., Nippert, J.B. & Collins, S.L. (2012) Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*, **93**, 697–703.

Redmond, K.T. (2009) Historic climate variability in the Mojave Desert. *The Mojave Desert* (eds D.L. Hughson, E.V. McDonald & D.M. Miller), pp. 11–30, University of Nevada Press, Reno.

Schwinning, S. & Hooten, M.M. (2009) Mojave desert root systems. *The Mojave Desert: Ecosystem Processes and Sustainability* (eds R.H. Webb, L.F. Fenstermaker, J.S. Heaton, D.L. Hughson, E.V. McDonald & D.M. Miller), pp. 278–311. University of Nevada Press, Reno.

Seager, R., Ting, M., Held, I., Yochanan, K., Lu, J., Vecchi, G. *et al.* (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*, **316**, 1181–1184.

Shreve, F. (1915) The vegetation of a desert mountain range as conditioned by climatic factors. *Carnegie Institute Washington Publication*, **217**, 1–112.

Shreve, F. & Wiggins, I.L. (1964) *Vegetation and Flora of the Sonoran Desert*. Stanford University Press, Stanford.

Smith, S.D., Monson, R.K. & Anderson, J.E. (1997) *Physiological Ecology of North American Desert Plants*. Springer-Verlag, Berlin.

Smith, S.D., Herr, C.A., Leary, K.L. & Piorkowski, J.M. (1995) Soil-plant water relations in a Mojave Desert mixed shrub community: a comparison of three geomorphic surfaces. *Journal of Arid Environments*, **3**, 339–351.

Smith, S.D., Huxman, T.E., Zitzer, S.F., Charlet, T.N., Housman, D.C., Colemanr, J.S., Fenstermaker, L.K., Seemann, J.R., & Nowak, R.S., (2000) Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. *Nature*, **408**, 79–82.

United Nations Convention to Combat Desertification (UNCCD) (1994) Elaboration of an international convention to combat desertification in countries experiencing serious drought and/or desertification, particularly in Africa. U.N. Doc. A/AC.241/27, 33 I.L.M. 1328. United Nations, New York.

United States Census Bureau (USCB) (2013) United States Census Bureau Population Estimates. available at http://www.census.gov/popest. Accessed January 3, 2014

United States Department of Agriculture (USDA) (2014) Plants Database. Available at http://plants.usda.gov Accessed January 3, 2014.

Walsh, C. & Mac Nally, R. (2009) hier.part: Hierarchical partitioning. R package version 1.0-3. crantastic.org/packages/hier-part/versions/1922.

Webb, R.H. & Wilshire, H.G. (1980) Recovery of soils and vegetation in a Mojave Desert ghost town, Nevada, USA. *Journal of Arid Environments*, **3**, 291–303.

Wood, Y.A., Graham, R.C. & Wells, S.G. (2005) Surface control of desert pavement pedologic process and landscape function, Cima Volcanic field, Mojave Desert, California. *Catena*, **59**, 205–230.

Young, M.H., McDonald, E.V., Caldwell, T.G., Benner, S.G. & Meadows, D.G. (2004) Hydraulic properties of a desert soil chronosequence in the Mojave Desert, USA. *Vadose Zone*, **3**, 956–963.